The Genetics and Evolution of Avian Migration

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One of the characteristics of avian migration is its variability within and among species. Variation in migratory behavior, and in physiological and morphological adaptations to migration, is to a large extent due to genetic differences. Comparative studies suggest that migratory behavior has rapidly and independently evolved in different lineages. One reason behind the high potential for de novo evolution of migratory behavior in sedentary populations seems to be the ubiquity of genetic variation for migratory traits in nonmigratory individuals. In resident lineages, a high degree of hidden genetic variation for migratory traits can be maintained because a migratory threshold determines whether migratory behavior is expressed. Genetic correlations among migratory traits and with other traits of the annual cycle are likely to play a major role in determining the rate and direction of evolutionary change.

Keywords: avian migration, quantitative genetics, adaptive evolution, phylogeny, genetic correlation

Migration is ubiquitous. Nearly every animal group capable of movement undertakes some kind of daily displacement or seasonal migration. Bird migration is probably the biological phenomenon that most fascinates and has attracted the most interest among nonscientists. For this reason, it has probably one of the longest traditions of scientific investigation in biology (Berthold 2001). One distinctive feature of avian migration is its diversity, which ranges from the spectacular mass migration of large soaring species such as storks to the almost invisible movements of some small passerines traveling silently and alone during the night hours. Thus, almost every population of migratory individuals differs to some extent from every other such population in its propensity to migrate, in migration timing, in migration route, or in how the migratory journey is done—for instance, whether in a few long stages or in many short hops.

Some general features are common to all migratory individuals—for instance, the suppression of maintenance activities or the deposition of energy reserves—and these features help to define migration and identify migratory individuals (Dingle 2006, Dingle and Drake 2007). Yet none of these features is unique to migratory birds (Piersma et al. 2005); similarly, there is probably no one "adaptive problem" for which only one solution has been realized. Thus, anyone observing and studying migration phenomena will perceive the diversity of migration and start asking questions about its plasticity, its persistence, and its evolution.

Why are there so many migration patterns? How did they evolve? Can the migratory strategies of a population change if environmental conditions change? Are these changes due to individual phenotypic adjustment, or do they result from evolutionary change? What are the limits of adaptation? In this article I would like to address these questions through a synthesis of what is known about the genetics and evolution of avian migration.

Ultimate causes for the evolution of migration

The selective advantages leading to the evolution of migratory movements have long been acknowledged. Migration is an adaptive response to seasonal environments, which allows animals to take advantage of spatial variation in the seasonal fluctuation of resources (Gauthreaux 1982, Rappole 1995, Berthold 1996). By using different areas during different times of the year, many bird species have been able to successfully colonize areas offering favorable conditions only during a short period. For instance, migratory birds breeding at high latitudes (e.g., in the arctic tundra) can take advantage of the extraordinary abundance of food during a few weeks in early summer and profit from long days, which allow them to extend foraging time. By leaving these areas after breeding, they avoid the uncertainties of northern winters with short days, low temperatures, and low food availability. Other ultimate factors favoring the evolution of migration include escape from inter- and intraspecific competition in saturated habitats and avoidance of predators and parasites (Alerstam et al. 2003).

In addition, intraspecific competition has been recognized as a particularly important determinant of avian migration

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patterns (Kalela 1954, Gauthreaux 1982). Assuming that the migratory trip is costly, we expect migration only in those individuals that incur a higher cost in terms of fitness by staying on the breeding grounds than by vacating them. Thus, subdominant and inexperienced individuals—that is, in a hierarchy, those least likely to get access to food resources and having the lowest probability of survival—will gain most from migrating (see also Kaitala et al. 1993). This factor is well illustrated among passerine birds, for even those that are considered completely resident (e.g., European tits of the genera *Parus* and *Cyanistes*) migrate in their first year but often remain on the breeding grounds during winter when they are older. In addition, females, which in most species are smaller than males, often tend to be more migratory than males (Ketterson and Nolan 1983, Berthold 1996, 2001). The ultimate cause for this difference in migratory behavior is attributed to the low competitiveness of juvenile birds and females, which results in low survival on the breeding grounds during the nonbreeding season when food is scarce.

Phylogenetic evidence for the evolutionary lability of migratory behavior

In recent years, the advent of molecular techniques and the improvement of statistical methods have boosted the use of phylogenetic and comparative approaches to reconstruct the evolution of complex traits (Martins 2000). By mapping the incidence of migration on molecular phylogenies, a number of phylogenetic studies have shown that migration has evolved repeatedly and very rapidly in different avian lineages (see, for instance, Helbig 2003, Outlaw et al. 2003, Joseph 2005, Davis et al. 2006). Using the phylogenies of the two Old World warbler genera *Sylvia* and *Phylloscopus,* Helbig (2003) showed that migratory species were distributed across varied branches of the phylogenetic trees and that in many cases, the closest relatives of migratory species were not other migratory species but sedentary ancestors. He concluded that these results provide strong evidence for an independent origin of migration in different, predominantly nonmigratory clades.

This pattern holds not only for variation of migratory status among species but also for differentiation within species. In the blackcap (*Sylvia atricapilla*), for instance, a large amount of geographic variation exists in migratory behavior. Populations in the northeastern part of the species' range (e.g., Scandinavia, Russia) are completely migratory and travel long distances. Populations at the southwestern end of the breeding range (e.g., Portugal, Spain) and on islands in the Atlantic Ocean (e.g., Cape Verde Islands) are sedentary. In between, one finds the whole range of migration strategies: middle- and short-distance migrants and populations where only part of the population migrates (Berthold 1988). A phylogeographic study of 12 blackcap populations from across the species' breeding range has revealed that migratory populations are not more closely related to one another than to sedentary populations, ruling out the possibility that migration evolved only once in this species (Pérez-Tris et al. 2004). Moreover, this study suggests that current migration patterns evolved very recently, probably during the species' postglacial expansion. In some blackcap populations, migration may have been lost again, after colonization of areas with mild winters.

Such complex phylogenetic patterns in the presence and absence of migratory behavior have also been found in several other species, such as Swainson's warbler (*Limnothlypis swainsonii*) or the black-throated blue warbler (*Dendroica caerulescens*). The colonization of new areas seems to have been the most important selective factor for the de novo evolution of migration or its loss in a lineage (Joseph et al. 2003, Outlaw and Voelker 2006).

New robust phylogenies based on a number of molecular markers and newly developed phylogenetic methods now make it possible to test hypotheses on the geographical and ecological factors determining the origin and evolution of avian migration (Zink 2002). This advance has led to new, more specific, and appropriate questions about the origin of avian migration, such as whether the origin of a clade and the origin of migration in this clade are identical (Joseph 2005).

The proximate causes of variation in migration

Among-species variation in migratory status and, in particular, geographic variation within species may have different proximate causes. Since populations of residents, short-distance migrants, and long-distance migrants often live in different habitats, different geographical regions, or both, whether a population is migratory or resident year-round could be determined simply by environmental conditions (e.g., day length, temperature, or food availability) in the breeding area during the nonbreeding season. As a consequence, among-population variation could be a direct response to the environment. Alternatively, migration could be endogenously determined by a genetic program (box 1), and geographic variation in migration could reflect genetic adaptation to different environments.

From an adaptive perspective, we expect genetic control of migratory behavior because organisms need to leave the breeding grounds before conditions deteriorate, that is, while conditions are still good enough to allow them to build up energy reserves. Moreover, in short-lived species such as many small passerines, mean life expectancy is less than two years, and most individuals will make only one return migration. As a result, the potential gain from experience is limited. A number of experimental studies have established that in this group of birds, among-species and among-population differences in migratory behavior and in traits of the migratory syndrome—including the circannual organization, orientation, and deposition of fat and protein reserves—are largely due to genetic differences (Berthold and Helbig 1992, Berthold 1996, 2001).

Within-population phenotypic variation in migratory behavior largely reflects genetic variation, yet nongenetic variance components, including environmental variation and variation in experience and condition, may also be important (Pulido and Berthold 2003, van Noordwijk et al. 2006). Long-lived species such as geese, storks, or cranes

Box 1. The genetic migration program.

During the time that their wild counterparts are migrating, captive birds from migratory populations show activity that, to a large extent, mirrors migratory behavior in the wild, particularly in hand-reared birds during their first migratory season (Berthold 1996). In nocturnal migrants, this migratory restlessness can be easily distinguished from other activities because it occurs only during the migration season. The patterns of this proxy for migratory activity indicate that migratory birds possess an innate program that “tells” them how fast to develop, when to leave the breeding area, how fast and in which direction to fly, and when to stop migrating (Berthold 2001). Guided by this “autopilot,” most inexperienced birds usually end up in appropriate wintering areas.

This migration program is largely insensitive to most environmental perturbations, whether wind, unfavorable weather conditions, or food scarcity, for which birds do not seem to compensate (Berthold 1996). Migrating birds may, in contrast, respond to magnetic cues (Fransson et al. 2001). At the end of the migratory journey, however, the program is likely to become more flexible, and birds may respond strongly to external cues such as food availability or habitat structure. They may thus extend or shorten migration until they find an area with favorable conditions (Terrill 1990). After the first migratory journey, the genetic program that guided a bird during its first trip probably does not come into play, or comes into play only under exceptional conditions. Once a bird has gained experience, it can take advantage of this knowledge and modify its behavior in response to displacements and environmental conditions. Moreover, experienced birds can use their internal map and compass to find their way from the wintering to breeding areas and back, as well as to the best stopover sites (Åkesson and Hedenström 2007).

These hypotheses raise a question: If migration as performed during the first migratory trip can be modified later, why is the migration program of evolutionary importance? Large-scale displacement experiments with starlings (*Sturnus vulgaris*) and other species, and analyses of ringing recoveries, suggest that the wintering area used by a bird in its first year—that is, the area chosen after the first migratory journey—is also used in subsequent seasons (Perdeck 1958, Mouritsen 2003). Thus, the first migratory trip, as determined by the genetic program, determines the wintering site used by each individual bird and each individual’s migration. By this mechanism, the genetic program and its variation measured in the laboratory become major determinants of phenotypic variation in migratory behavior and evolutionary processes in the wild.

migrate in groups and are guided by the oldest, most experienced individuals. In these species, the genetic program, although still present (see, for instance, Chernetsov et al. 2004), seems to play only a minor role in determining variation in migration. This cultural transmission of migration may facilitate very rapid changes in migratory behavior (Sutherland 1998), although the adaptive response in such species is not necessarily faster than in organisms in which migration is controlled primarily by a genetic program (van Noordwijk et al. 2006).

The evolution of migration in resident populations and of residency in migratory populations

If the propensity to migrate or to remain sedentary can evolve in a short time, as suggested by recent comparative studies, genetic variation for migratory behavior must exist even in populations that do not show any apparent phenotypic variation, that is, populations in which all individuals stay on or leave the breeding area during the nonbreeding season.

The genetic explanation for the evolutionary lability of migratory behavior in birds can be derived directly from the mode of inheritance of migratory activity, which is best described by the threshold model of quantitative genetics (figure 1; Pulido et al. 1996, Roff and Fairbairn 2007). If the propensity to migrate is determined by a continuous variable and a threshold that determines whether migratory activity is expressed, it is highly unlikely that migratory traits will be fixed, even under strong, persistent directional selection. The reason is that if residency is favored, the distribution of migratory activity will shift below the threshold, and migratory traits will not be phenotypically expressed. In resident populations, this genetic variation is therefore not exposed to natural selection and cannot be easily eliminated, unless the traits in question are genetically correlated to other, phenotypically expressed traits that are under selection.

Most likely, this reservoir of cryptic variation in residents underlies the recurrent expression of migratory behavior in apparently nonmigratory populations. As a consequence, most, if not all, resident populations are to some extent migratory—that is, they consist of residents and a small fraction of migratory individuals—and this mix may facilitate the rapid evolution of adaptive migration patterns (Berthold 1999). Likewise, genetic variation in other components of the migratory syndrome (e.g., orientation mechanisms, spatiotemporal program, response to photoperiod) may persist in large, nonmigratory populations for thousands of generations if the traits are not phenotypically expressed. Nevertheless, because they are present in most bird species, irrespective of the species’ propensity to migrate, the traits are likely to remain functional.

Support for this hypothesis comes from the rapid evolution of migration in sedentary populations in the wild (Berthold 1996). The best-documented example for such an evolutionary process is found the house finch (*Carpodacus mexicanus*). After the introduction of this western North American resident species to eastern North America in 1940, the newly founded population grew rapidly, expanded its range, and in large parts of its new breeding area became mi-

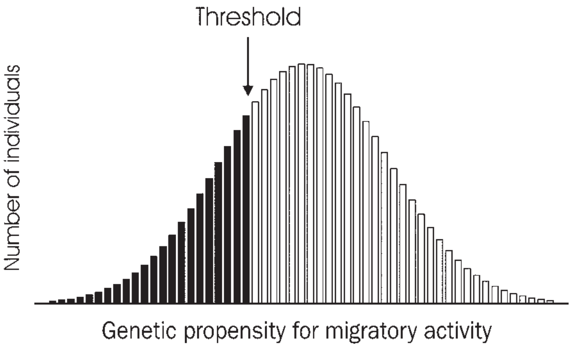

Figure 1. The threshold model of migration, representing the distribution of migratory activity in a partially migratory population. One part of the population migrates (white bars); the other part is resident (black bars). A threshold determines whether the genetic predisposition to migrate is expressed. Individuals below the migration threshold do not express migratory activity and do not show any phenotypic variation, though genetic variation for migratory activity does exist among these nonmigrants.

gratory (Able and Belthoff 1998). Further indirect evidence supporting this hypothesis is the remnant migratory restlessness found in some resident bird populations (e.g., Pulido and Berthold 2004, Helm and Gwinner 2006) and the adaptive response to seasonal changes in day length found in tropical populations of migratory birds (Styrsky et al. 2004, Helm et al. 2005).

The evolutionary process leading from complete migratoriness (i.e., the state in which all individuals migrate) to complete residency (i.e., the situation in which no individual migrates) can be described by the same model. Residency can evolve in any population after an environmental change favoring shorter migration distance. As the distribution of migration distances shifts toward the threshold, and the mean distance migrated by each migratory individual decreases, the number of nonmigratory individuals gradually increases. The transition from a migratory to a sedentary population will thus result in partially migratory populations with gradually decreasing migration distances and increasing proportions of resident individuals.

This process has been demonstrated in a large-scale selection experiment in the blackcap, in which individuals from a partially migratory population were selectively mated according to their migratory status; that is, migrants were mated with migrants and nonmigrants with nonmigrants (Berthold et al. 1990). In the nonmigratory line, the frequency of resident individuals increased, while the amount of migratory activity shown by the migratory individuals gradually decreased. In the migratory line, the proportion of migrants significantly increased, as did the amount of activity in the migrants (figure 2). A further analysis revealed that the likelihood of producing nonmigratory offspring was determined not only by the (measurable) amount of migratory activity produced by the parents—parents with low mean activity were significantly more likely to have nonmigratory offspring—but also by the generation of selection. This result suggests that selection not only changed the mean level of migratory activity but also shifted the migration threshold. Further evidence for genetic variation in the position of the migration threshold was provided by a series of common garden experiments in blackcaps. Under identical experimental conditions, migratory blackcaps from three partially migratory populations (Madeira, Canary Islands, and Cape Verde Islands) produced about the same mean amount of migratory activity but differed markedly in the proportions of individuals showing this activity (Pulido et al. 1996).

Evidence for environmental influence on the position of the migration threshold comes from observations in the wild. In populations of facultative partial migrants, only part of the population migrates, while the other fraction remains on the breeding grounds. The proportion of migrants, which may

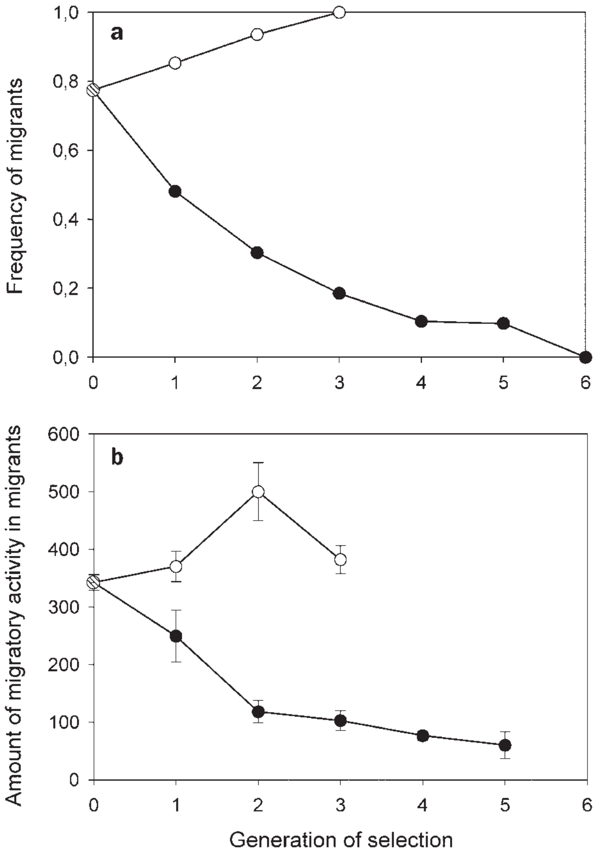

Figure 2. Direct response of the frequency of migrants (a) and correlated response of the amount of migratory activity in migrants (b) to artificial selection for higher (white dots) and lower proportion of migrants (black dots) in a partially migratory blackcap population from southern France. The strong correlated selection response indicates that incidence and amount of migratory activity are tightly genetically correlated (data from Berthold et al. 1990 and Pulido et al. 1996).

range from zero to one, varies from year to year and is determined by actual environmental conditions, such as breeding density or food availability (e.g., Nilsson et al. 2006). The more migratory a population becomes, however—as expressed, for instance, by increasing migration distance—the smaller the influence of environmental factors in the expression of migratory behavior seems to be. This buffering of environmental variation in the expression of migratory traits is probably characteristic of long-distance migrants (Pulido and Widmer 2005; see below). Strong selection for migration in these species and populations seems to drive a process of genetic assimilation (Pigliucci and Murren 2003), whereby the expression of a trait becomes independent of the environmental trigger.

The evolutionary significance of the response to day length

Migrants are under strong selective constraints. For migration to be successful, birds need to be at suitable places when these places offer the most favorable conditions, a need requiring an optimization of migratory movement in space and time. Of course, conditions vary not only from season to season but also from year to year, and the optimal conditions for reproduction may shift over time. Nevertheless, every year the best environmental conditions will prevail during a particular period, which is often predictable.

Because migrants, particularly birds migrating over large distances, lack information on the conditions at their destination, they are guided not only by their internal genetic program but also by day length. This highly predictable and reliable cue helps the birds to time the start of their migratory journey in such a way that they will encounter favorable environmental conditions on arrival up to thousands of miles away in their reproductive or wintering area. Moreover, birds use day length to adjust other life history events, such as the timing and intensity of molt (which needs to be completed before migration) and the timing of reproduction, in response to whether a bird winters or breeds in the north or south, and clutch size, in response to whether a bird breeds early or late in the season. This reaction norm may allow birds' annual cycle to respond adaptively to shifts in both the breeding and the wintering areas (as might occur after displacements by winds or because of genetic change in migration distance) without requiring evolutionary modification of the time program (Coppack and Pulido 2004). Response to photoperiod is not an idiosyncrasy of migratory birds but, like many other traits constituting the migratory syndrome, a feature common to all birds. In migrants, however, the response to day length seems to be of particular adaptive importance and may predominate in the control of juvenile development, molt, and migration timing and expression and in the modification of reproductive traits (Berthold 1996). This photoperiodic response may partly be lost, however, in populations living in highly unpredictable environments where day length is not a reliable cue to food availability, as in high mountain habitats (Widmer 1999). In blackcaps, among-family variation in the response to changes in day length suggests that rapid evolutionary change in phenotypic plasticity may be possible (Pulido et al. 2001a, Coppack et al. 2001).

Genetic variation in migratory traits

Genetic variation is ubiquitous in all classes of traits, but the amount of variation may differ. Evolutionary theory predicts that if traits persistently experience strong directional selection, genetic variation will be lost. Complex traits will show high levels of genetic variation. Traits closely correlated with fitness, such as most reproductive traits, actually have low heritability and high additive genetic variation. In contrast, traits with low correlation to fitness, such as many morphological traits, generally show high heritability and low levels of environmental variation (Merilä and Sheldon 1999).

Traits of the migratory syndrome generally correspond to these patterns. Morphological traits of the migratory syndrome, like wing length or wing shape, have higher heritability than components of migratory behavior or physiological traits. These latter features have moderate heritability, typical of behavioral and physiological traits (Pulido and Berthold 2003). The mean heritability (h^2) of components of migratory behavior in birds, such as timing, prevalence, and amount of migratory activity, is 0.37 (standard deviation [SD] = 0.23, $n = 20$). There is no significant difference between traits related to the timing of migration ($h^2 = 0.34$, SD = 0.24, $n = 12$) and traits related to the amount of migratory activity ($h^2 = 0.41$, SD = 0.22, $n = 8$).

The reliability of heritability estimates for the incidence, amount, and timing of autumn migration in the blackcap has been confirmed in artificial breeding experiments (Berthold et al. 1990, Pulido et al. 1996, Pulido et al. 2001b), where selection responses were found to agree with predictions derived from the breeder's equation, that is, the product of heritability and selection intensity (Roff and Fairbairn 2007). Under strong selection, migratory traits can change in a few generations. In a migratory blackcap population, for instance, two generations of artificial directional selection delayed mean autumn departure date from the breeding grounds by more than a week (Pulido et al. 2001b). Rapid genetic changes have also been observed in the wild. In a population of cliff swallows (*Petrochelidon pyrrhonota*) in Nebraska, for example, an extended period of cold weather in spring caused high mortality among individuals that had arrived early. This strong selection delayed spring arrival in the population significantly (Brown and Brown 2000).

Populations differing in migratory strategy—this difference presumably reflecting differences in the direction and strength of selection—are excellent subjects for studying the effects of selection on genetic variation in migratory traits. One prediction is that populations of long-distance migrants that are present on the breeding grounds during a very short period—and therefore under strong stabilizing selection for traits determining the timing of migration—will maintain less additive genetic variation than populations with weaker time constraints. In a comparative study, we tested this hypothesis at both an intraspecific and an interspecific level in European *Sylvia* warblers (Pulido and Widmer 2005). In a common garden experiment, we kept garden warblers (*Sylvia borin*), long-distance migrants from mountain and lowland populations that differed in the length of the breeding season by about a month, and blackcaps from a population migrating considerably shorter distances in captivity under identical conditions and measured their timing of migratory activity. We found no evidence for reduced genetic variation in the onset of migratory activity in the populations with stronger time constraints. Nevertheless, the study clearly revealed reduced environmental variation in the long-distance migrant (the garden warbler) as compared with the middle-distance migrant (the blackcap; figure 3).

This result is in line with a comparison of published estimates of migration timing heritability in birds suggesting that long-distance migrants, if differing at all, have higher heritability ($h^2 = 0.39$, SD = 0.27, $n = 6$) than short-distance migrants ($h^2 = 0.30$, SD = 0.23, $n = 6$), although this difference is not statistically significant. As a consequence of this canalization of phenotypic traits, the response to selection may be stronger in long-distance migrants than in short-distance migrants, because selection will act on the genetic and not the environmental component of variation. It is very likely that this buffering of environmental variation in traits under strong selection, as found in long-distance migrants, is a general feature of many migratory organisms.

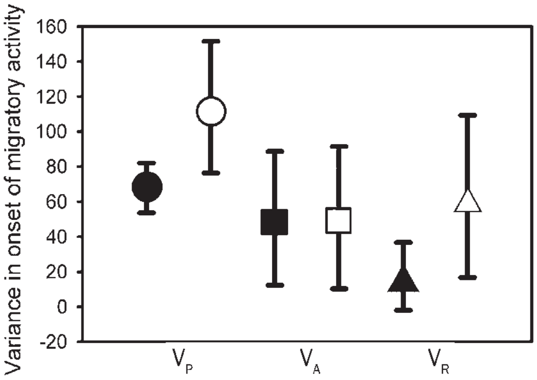

Figure 3. Variance components of the onset of autumn migratory activity in a garden warbler (black) and a blackcap (white) population. Populations do not differ in the amount of additive genetic variance (V_A), but differ significantly ($p < .05$) in the amount of total phenotypic (V_P) and residual (i.e., environmental, V_R) variance (data from Pulido and Widmer 2005).

Genetic correlations

Migration is a trait complex that integrates many different characters, including behaviors, physiology, morphology, and life histories, into a syndrome (Dingle 2006, Dingle and Drake 2007). One particular characteristic of migration, like that of other behavioral syndromes or complex traits, is a high level of integration among single traits; in other words, the expression of one trait covaries with the expression of another trait (Pulido and Berthold 1998). This covariation is highly adaptive because, for example, migratory activity carries an advantage to an individual only if that individual also possesses the appropriate orientation, timing, and physiological mechanisms needed to undertake migration successfully and to find suitable wintering sites.

De novo evolution of and evolutionary changes in the migratory syndrome follow the same processes that determine the evolution of other complex traits (Frazzeta 1975): Whenever selection persistently favors the simultaneous optimization of multiple traits, genetic correlations among these traits will evolve. To the extent that genetic correlations among migratory traits have been studied, it has become apparent that genetic correlations are major determinants of evolutionary trajectories of migratory traits (Pulido and Berthold 1998, 2003). Correlations among migratory traits seem to be determined by the major axis of environmental change, which, for most migratory birds breeding in the temperate zone, is the increase and decrease in temperature. Low temperatures generally favor long migration distances, with short stays on the breeding grounds and an increase in migration propensity, including an increase in the amount of reserves accumulated. Higher temperatures favor a decrease in migration propensity (Berthold 2001, Pulido and Berthold 2004).

Genetic correlations among concomitantly optimized traits favor a rapid response to changes along this environmental axis. Thus, if global temperatures increase, selection will favor wintering in areas closer to the breeding grounds, later departure from and earlier arrival at the breeding grounds, lower fat loads, and other concomitant changes in morphology and life history, such as larger clutches, more broods, or rounder wings. If the signs of the genetic correlations are in accord with the correlations of the selection vectors, adaptive changes in these traits will be determined not only by direct selection on the traits themselves but also by selection on other traits of the migratory syndrome. The resultant response to selection along this environmental axis may be very strong, as predicted for the incidence and timing of autumn migration and migration distance (Pulido and Berthold 1998, 2003).

If, however, selection favors multivariate character states outside this environmental axis—for instance, early arrival on the breeding grounds and long migration distance—genetic correlations will slow or even prevent multicharacter adaptation (Pulido and Berthold 1998). Recently, such genetic constraints on adaptation to climate change have been found in the blackcap for the joint adaptation of timing of egg laying and timing of autumn migration (Coppack et al. 2001) and for evolutionary change in the onset of autumn migration in relation to the timing of juvenile molt (Pulido and Coppack 2004). Moreover, heterogeneous patterns of climatic change along the migratory route—for example, an increase in temperatures on the breeding grounds and a decrease in the wintering areas—will result in selection regimes that most bird populations have not previously experienced, at least in recent times. As a consequence, the selective response will be hampered rather than reinforced by extant genetic correlations among migratory traits.

It is currently not completely clear which traits of the migratory syndrome are integrated and which characters will evolve independently. In birds, some evidence indicates that not all traits are equally likely to covary genetically. Behavioral and physiological traits that are directly linked to the migratory journey—including the amount and timing of migratory activity, the timing of molt, the endogenously preferred direction of movement, and the amount of energy stored before the migratory journey—seem to be strongly correlated (Helbig 1996, Pulido and Berthold 2003, Pulido and Coppack 2004). Other characters of the migratory syndrome, such as morphological and life-history traits (Dingle 2006, van Noordwijk et al. 2006), do not tend to covary genetically with migratory behavior, or do so only loosely. We generally expect strong integration of traits within functional complexes (e.g., orientation, timing, flight morphology, migration physiology) but weak or missing coherence among traits from different complexes (Pulido and Berthold 2003). As a consequence of different selection regimes and constraints, we further expect the delimitation of functional complexes and the degree of integration within and among complexes to vary among populations differing in migration strategy and habitat. Integration will probably be higher in long-distance migrants than in short-distance migrants, since long-distance migrants are subjected to stronger selection and constraints on traits of the migratory syndrome.

Rapid changes in migratory behavior: The blackcap as a case study

In the past decades, a large and convincing body of evidence has accumulated to demonstrate that migratory traits—or at least the behavioral components of the syndrome, such as the propensity to migrate, migratory direction, and the timing of migration—can change rapidly (Fiedler 2003, Lehikoinen et al. 2004, Pulido and Berthold 2004). This phenomenon has been particularly well studied in passerine birds that have responded to recent global increases in temperature by arriving earlier on the breeding grounds, shortening migration distances (a consequence of shifts of the wintering areas), and increasing the proportion of resident individuals (Fiedler 2003). These changes may be partly due to plastic individual adjustments of behavior, as suggested by some studies reporting changes in migration phenology (Marra et al. 2005, Hüppop and Winkel 2006) and the dependence of migration speed on physiological condition (Newton 2006). Migrants thus seem to be capable of adjusting their migration speed on the journey from the wintering to the breeding areas—and ultimately their arrival at their destination—according to the climatic conditions en route. It is currently unclear whether this flexibility in migration speed is based on individual decisions, on constraints in the migration physiology that could limit migration speed under unfavorable conditions, or on environmental cues that trigger modifications of the migration program (i.e., on phenotypic plasticity). Unfortunately, experimental studies investigating the mechanism of these adjustments are still scarce (Coppack and Both 2002, Coppack and Pulido 2004).

In addition to flexible individual modification of migratory behavior, evolutionary change in response to natural selection is a major mechanism for the adaptation of the components of the migratory syndrome to changes in the environment (Pulido and Berthold 2004). The best-documented instance of evolutionary change in migratory behavior is the recent establishment of a new wintering area by the blackcap warbler. Central European populations of this species traditionally winter to the southwest of their breeding grounds in the western Mediterranean region. In the past four decades, the number of birds wintering in Britain and Ireland, located about 1500 km to the north of the blackcaps' traditional wintering grounds, has been steadily increasing (Berthold and Terrill 1988). These birds are not British breeding birds that stay on the breeding grounds over winter; rather, they come from central European populations that have established a new wintering area. Migration to this new area involves a shortening of the mean migration distance by about 50% and a shift of the mean migratory direction by about 70° (Berthold et al. 1992). A number of factors may be driving this evolutionary process, including more birds surviving the winter in the British Isles because humans feed them; the availability of more garden plants with winter fruit; and, at least in the last two decades, warmer winters than in the past (Berthold and Terrill 1988, Berthold 1996).

Changes in migration have been accompanied by large potential fitness benefits: Because of the shorter migration distance, birds wintering in the northwest save energy and time. Moreover, because of rapidly shortening days in autumn, very short days in winter, and a rapid increase in day length in spring, developmental processes such as gonadal growth, body molt, and the accumulation of fat and protein deposits are strongly accelerated, allowing birds wintering in the north to migrate and finally to breed earlier than individuals spending the winters on the traditional wintering grounds in the Mediterranean region (Terrill and Berthold 1990, Coppack and Pulido 2004). As a result of earlier breeding, being in better condition, and possibly occupying the best territories, blackcaps wintering in the north produce more young, which are likely to be in better condition (Berthold and Terrill 1988, Bearhop et al. 2005).

The rapid evolution of a new wintering area has probably been possible only because of restricted gene flow among individuals that differ in migratory behavior. Blackcaps wintering in Britain breed about two weeks earlier than blackcaps wintering in southwestern Europe or northern Africa. Since males that arrive early are most likely to mate with females that arrive early and therefore hardly interbreed with late-arriving individuals, and since wintering area is associated with arrival date, assortative mating with regard to arrival date imposes a barrier to gene flow. This process makes it possible to evolve rapidly and to maintain alternative wintering strategies in one blackcap population (Bearhop et al. 2005). Assortative mating resulting from habitat segregation has also been suggested as a potential mechanism that separates blackcaps differing in migration strategy within one partially migratory population (Berthold 1986). Assortative mating with regard to arrival date and breeding habitat stemming from different temporal and spatial windows for reproduction is probably a common mechanism facilitating the maintenance and evolution of different migration strategies in populations of migratory organisms like birds.

Constraints on evolutionary change

Although a large body of evidence indicates that bird populations can readily adapt migration to changes in environmental conditions, a number of studies suggest that in some species, adaptive modifications of migration patterns may not occur or may occur only slowly. Indeed, it has long been recognized that some migration routes may not be optimal. Some populations do not migrate to the closest suitable wintering area; other populations migrate on unexpectedly long routes that seem to be detours. It is assumed that these bird populations currently use historical migration routes because of some kind of constraint.

Sutherland (1998), for instance, found 43 examples of bird populations that had recently changed their migration routes, while 14 populations continued to migrate on apparently suboptimal routes. He found maladaptive migration patterns only in species with a short duration of parental care, specifically, small passerines for which we know that migration patterns are predominantly genetically controlled (Berthold 2001). In species with extended parental care—that is, species with culturally transmitted migratory behavior—changes occurred often, and no suboptimal migration routes were found. This result may indicate that some changes in the migration program, specifically in migration direction, may be difficult to accomplish genetically. Biogeographic studies comparing range sizes and distributions of migratory and resident birds species come to similar conclusions. While the extension of breeding ranges along the migratory axes does not differ between migratory and resident bird species, range extensions orthogonal to the migratory routes are more limited in migrants (Böhning-Gaese et al. 1998, Bensch 1999), although this limitation does not hold for the nonbreeding ranges (Thorup 2006). These observations, of constraints in range expansions as well as the low success rate in introductions of migratory birds (Sol and Lefebvre 2000), suggest that some complex changes in migration may not be possible, or take place very slowly, probably hindered by antagonistic genetic correlations.

Indirect evidence for evolutionary stasis in migratory traits also comes from phylogeographic studies suggesting that differences in migratory patterns among populations have been maintained for thousands of generations, since the late Pleistocene (Baker 2002). In Swainson's thrush (*Catharus ustulatus*), for instance, individuals breeding in different parts of the breeding range differ in migration route and wintering area. Birds breeding in Alaska fly westward great distances before they turn south; on the other side of a migratory divide, thrushes of the coastal population fly southward. Using mitochondrial DNA haplotype differences between populations, Ruegg and Smith (2001) demonstrated that the Alaskan population is genetically closely related to the continental group and that this population was established after a recent range expansion. The apparent detour of this population most probably reflects its colonization route (Ruegg et al. 2006), and the most likely explanation therefore seems to be that a more direct migration route could not evolve. A number of different explanations exist for evolutionary stasis, however, of which the lack of genetic variation is only one possibility (Merilä et al. 2001). The investigation of these explanations requires long-term population studies assessing selection regimes, genetic variation, and the interaction of genotypes and environment (Pulido and Berthold 2003).

One factor that has been identified as a major constraint on the evolution of new migration patterns is the presence of large ecological barriers, such as oceans and deserts, which may prevent shifts in breeding and wintering ranges (Henningsson and Alerstam 2005). To overcome these ecological barriers requires large "evolutionary jumps" in migratory behavior, which may take a very long time and are likely only in the presence of large amounts of genetic variation. The need for such jumps has been identified as one potential major constraint on the evolution of residency in long-distance migrants crossing the Sahara desert (Pulido et al. 1996).

Outlook

Although avian migration is probably one of the best-studied biological phenomena in nature, and the development of theories on its evolution and maintenance has a long tradition (Alerstam and Hedenström 1998), our knowledge about the genetic architecture of the migratory syndrome is limited, and the implications of that architecture for the evolution of migration have only recently been considered. The study of the causes of individual variation in migration is a relatively neglected field (van Noordwijk et al. 2006). Practically all of our present knowledge on the genetics of migration is based on experimental studies in a few model species—the blackcap being by far the best studied—all of which are passerines breeding in the Western Palaearctic and wintering in southern Europe or northern Africa.

This geographic scope may limit the ecological conditions studied and the evolutionary processes scrutinized. In addition, these species represent only a limited range of the migration strategies realized in birds. Most of the investigated species travel alone at night, using flapping flight. Yet many avian species (e.g., seed-eating birds like most finches or grazing birds like geese and ducks) migrate during the day and in flocks of conspecifics, and in the largest species, such as storks and cranes, soaring flight is the most important means of locomotion. In these species, the importance of the inherited migration program in the expression of an individual's migratory journey may be smaller, and the importance of learning and the social transmission of migratory behavior may predominate. As a result, we expect phenotypic changes in migration to have different dynamics than in the classical model species.

The study of the evolution of migration has been biased not only by limitations in which species have been investigated but also by a Northern Hemisphere perspective. Consequently, in early theories on the evolution of migration, the importance of selection outside the breeding area was underestimated or totally ignored (Rappole 1995). Today it is generally acknowledged that to understand adaptations in migration and their evolutionary change, we need to look at a birds' complete annual cycle, including migration and life-cycle events that take place on the wintering site. The first in-depth studies confirm that conditions on the wintering sites and during migration may be major determinants of migration and subsequent breeding success (Norris 2005, Studds and Marra 2005).

Thus, to test the validity of current hypotheses on the evolutionary genetics of avian migration, we need to extend our study of the genetics of migration to species whose migration strategies differ from those of previously studied species (e.g., diurnal migrants) or that represent different migration systems (e.g., austral migrants). Future research should further try to gauge the correlation among events on the wintering grounds, staging areas, and breeding sites and to assess the impact of these events on environmental and genetic variation and covariation among migratory and other life-history traits. New techniques, particularly those that make use of stable isotopes and trace elements, and the refinement of tracking technologies hold great promise to help us to test theories about the evolution of migration by making it possible to identify staging and wintering sites, as well as the habitat quality experienced by individual birds.

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